Impact of Grazing Intensity during Drought in an Arizona Grassland

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Abstract: The ecological benefits of changing cattle grazing practices in the western United States remain controversial, due in part to a lack of experimentation. In 1997 we initiated an experimental study of two rangeland alternatives, cattle removal and high-impact grazing, and compared grassland community responses with those with more conventional, moderate grazing practices. The study was conducted in a high-elevation, semiarid grassland near Flagstaff, Arizona (U.S.A.). We conducted annual plant surveys of modified Whittaker plots for 8 years and examined plant composition shifts among treatments and years. High-impact grazing bad strong directional effects that led to a decline in perennial forb cover and an increase in annual plants, particularly the exotic cheatgrass (Bromus tectorum L.). A twofold increase in plant cover by exotic species followed a severe drought in the sixth year of the study, and this increase was greatest in the high-impact grazing plots, where native cover declined by one-half. Cattle removal resulted in little increase in native plant cover and reduced plant species richness relative to the moderate grazing control. Our results suggest that some intermediate level of cattle grazing may maintain greater levels of native plant diversity than the alternatives of cattle removal or high-density, short-duration grazing practices. Furthermore, episodic drought interacts with cattle grazing, leading to infrequent, but biologically important shifts in plant communities. Our results demonstrate the importance of climatic variation in determining ecological effects of grazing practices, and we recommend improving conservation efforts in arid rangelands by developing management plans that anticipate this variation.

Keywords: *Bromus tectorum*, cheatgrass, climatic variation, exotic plants, livestock grazing, plant community, plant cover, short duration grazing

Impacto de la Intensidad de Pastoreo durante la Sequía en un Pastizal de Arizona

Resumen: Los beneficios ecológicos del cambio de prácticas de pastoreo de ganado en el oeste de Estados Unidos aun son controversiales, en parte por la falta de experimentación. En 1997 iniciamos un estudio experimental de dos alternativas, remoción de ganado y pastoreo de alto impacto, y comparamos las respuestas de la comunidad de pastizal con las de prácticas de pastoreo moderadas, más convencionales. El estudio se llevó a cabo en un pastizal semiárido, de alta elevación, cerca de Flagstaff, Arizona (E.U.A.). Durante 8 años realizamos muestreos anuales de plantas en parcelas Whittaker modificadas y examinamos los cambios en la composición de plantas entre tratamientos y años. El pastoreo de alto impacto tuvo dos efectos direccionales que llevaron a una declinación en la cobertura de bierbas perennes y al incremento de plantas anuales, particularmente de pasto exótico Bromus tectorum L. Después de una sequía severa la cobertura de especies exóticas incrementó al doble en el sexto año del estudio, y este incremento fue mayor en las parcelas de pastoreo de alto impacto, en las que la cobertura de especies nativas declinó a la mitad. La remoción de ganado resultó en un leve incremento en la cobertura de plantas nativas y redujo la riqueza de especies de plantas en relación con el control con pastoreo moderado. Nuestros resultados sugieren que algún nivel intermedio de pastoreo puede mantener mayores niveles de diversidad de plantas nativas que las alternativas de remoción de ganado

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o de prácticas de pastoreo de alta densidad y corta duración. Más aun, las sequías episódicas interactúan con el pastoreo de ganado, conduciendo a cambios, poco frecuentes pero biológicamente importantes, en las comunidades de plantas. Nuestros resultados demuestran la importancia de la variación climática en la determinación de los efectos ecológicos de las prácticas de pastoreo, y recomendamos el mejoramiento de los esfuerzos de conservación en llanuras áridas mediante el desarrollo de planes de gestión que anticipen esta variación.

Palabras Clave: Bromus tectorum, comunidad de plantas, cobertura de plantas, pastoreo, pastoreo de corta duración, plantas exóticas

Introduction

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Scientific information on the effects of livestock grazing is plentiful and can be construed to support the claims of very different positions on the subject (e.g., Fleischner 1994; Brown & McDonald 1995). To improve the science of rangeland conservation, we argue for greater attention to the variability among ecosystems and experimentation with alternative grazing practices. Differences in site productivity and plant tolerance to grazing are great, even among similar grassland biomes (Mack & Thompson 1982), and responses to grazing vary with climatic conditions (Curtin 2002). Consequently, the evaluation of the effects of livestock on critical components of biological diversity and rangeland productivity may require regional- or site-specific research that incorporates climatic variability. Moreover, published research is based largely on observational studies that singularly address cattle removal as an alternative to current practices (Curtin 2002). Experimentation with management-relevant treatments provides an opportunity to establish predictable relationships among a variety of grazing practices and ecological responses, thus expanding conservation-based management beyond a single strategy.

Numerous alternatives to current grazing practices exist, including removing or reducing cattle (Bock et al. 1993), development of exurban housing (Maestas et al. 2003), and increasing the density of cattle (Savory & Parsons 1980). Fleischner (1994) highlights the negative effects of cattle and posits that their removal would benefit ecosystems at multiple trophic levels. Nevertheless, the ecological literature from the western United States provides contradictory evidence on the effects of removing livestock, particularly for plant communities (Brown & McDonald 1995; Curtin 2002). Stohlgren et al. (1999) compared grazed pastures with livestock exclosures in four western states and found no consistent effect of grazing on species diversity. Jones (2000) reviewed 150 studies of grazing in arid regions and found that the majority of research provides limited inference due to poor experimental design. Of the studies deemed sufficiently robust, vegetation responses were too varied to support a definitive conclusion on the effects of livestock removal (Jones 2000). In this journal Curtin (2002) reviewed recent grazing studies (Milchunas & Lauenroth 1993; Stohlgren et al. 1999; Jones 2000) and concluded that (1) because grassland ecosystems are sustained through dynamic processes of disturbance, research should broaden beyond exclosure-only studies; (2) climatic patterns, particularly in arid regions, often interact with management actions, necessitating the integration of treatment and climate effects in research; and (3) research should aim to identify environmental thresholds at which management actions have predictable effects.

Consistent with Curtin's (2002) recommendations to assess the conservation implications of alternative grazing practices, we examined a gradient of grazing intensities applied in an 8-year controlled experiment over a period of marked climatic variation. In a high-elevation semiarid grassland, we addressed the following questions: (1) What are the relative effects of alternative grazing practices and interannual climatic variation on the organization of grassland communities? (2) How do plant functional groups respond to cattle removal in contrast to increasing cattle density? and (3) What are the conservation implications of shifts in plant composition in a region where interannual climatic variation is great? We interpreted our results in the context of the published literature and make recommendations regarding the conservation of semiarid rangelands.

Methods

Study Area

The study site is located in a high-elevation, semiarid grassland in north-central Arizona (U.S.A., 34° 59′ 03′N 111° 26′ 30′W) at an elevation of 2160 m, within the upper Great Basin grassland (Brown 1994) at an ecotone that includes ponderosa pine (*Pinus ponderosa* P. & C. Lawson) and one-seed juniper (*Juniperus monosperma* [Engelm.] Sarg.). The herbaceous plant community is dominated by the perennial grasses western wheatgrass (*Pascopyrum smithii* [Rydb.] A. Löve) and squirreltail grass (*Elymus elymoides* [Raf.] Swezeyi) and the forb Carruth's sagewort (*Artemisia carruthii* Wood ex Carruth.). The soils are Mollisols dominated by shrink-swell clays with

Table 1. Water-year precipitation for the years when plant surveys occurred near Flagstaff, Arizona, and the difference from the 20-year mean of 384.2 mm.*

Year	Water-year precipitation (mm)	Difference from 20-year mean (mm)		
1997	172.2	-212.0		
1998	321.8	-62.4		
1999	194.1	-190.1		
2000	172.0	-212.2		
2001	230.9	-53.3		
2002	71.4	-312.8		
2003	188.0	-196.2		
2004	205.7	-178.4		

^{*}Water-year precipitation was calculated as the sum of precipitation 8 months prior to July.

basalt cobbles throughout. The variation of sand, silt, and clay textural classes was generally within a range of 10% among study plots (Loeser et al. 2001b). A full description of the study area and experimental design is in Loeser et al. (2001a).

The region has a biannual precipitation regime with winter snowfalls and summer rains. The area's 20-year mean for precipitation during the water year (8 months prior to July and our annual plant survey) is 384 mm. Water-year precipitation for this region during the years of this study, 1997–2004, was approximately one-half of the 20-year mean (Table 1). July is the warmest month of the year with a mean monthly maximum temperature of 27° C, and January is the coldest month with a mean minimum temperature of -9° C.

The history of livestock grazing for this site was difficult to document; however, available records indicate that low- to moderate-intensity livestock grazing has occurred on the site for the latter half of the twentieth century. Historical records suggest overgrazing occurred over much of Arizona between 1870 and 1890 (Hastings & Turner 1965; Curtin et al. 2002), and we expect this particular study site was no exception. Cattle and sheep grazing during 1900-1950 was variable, with generally greater stocking rates than in recent decades. In addition to livestock, large grazers, including elk (Cervus elaphus), mule deer (Odocoileus hemionus), and pronghorn (Antilocapra americana), inhabit this region and were not intentionally excluded from any treatment. Fecal counts suggest no difference in wild ungulate usage of experimental plots (Loeser et al. 2005).

Experimental Design

To document the relationships between grazing and the plant community, we implemented two alternative treatments in an area with preexisting grazing by cattle. We first selected a 320-ha pasture that received livestock grazing of moderate intensity (1 cow-calf pair/ha for 20 days/year in a rest-rotation cycle) in which ranchers man-

aged livestock to remove no more than 50% of above-ground plant biomass. The herd primarily comprised cow-calf pairs of a hybrid breed (Gelbvieh and Angus) that were habituated to the rest-rotation practice and the vegetation type. We built three 1-ha livestock exclosures adjacent to 1-ha livestock enclosures (three pairs). Adjacent to each fenced pair of plots, we demarcated a survey plot in the surrounding moderately grazed pasture (Fig. 1).

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In this manner the study site consisted of three blocks located in areas dominated by grassland vegetation with sparsely distributed trees. Each block contained three treatments (cattle removal, moderate grazing, high-impact grazing). The cattle removal and highimpact treatments were initiated in 1997. The moderate grazing practice was the experimental control because it was most similar to predominant land-use practices in the American southwest and was the initial condition of the novel treatments. The livestock enclosures received a high-impact, short-duration grazing treatment to simulate herd impact without killing plant root systems (average grazing event of 200 cow-calf pairs/hectare/year for approximately 12 hours). This treatment occurred annually except for 2002, when drought conditions forced ranchers to relocate their cattle. This treatment served as a critical upper-end treatment representing a ranching practice that could be implemented with open-range herding or similar concentrated techniques.

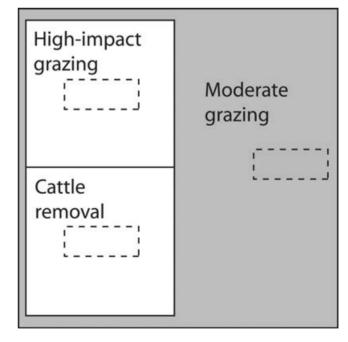


Figure 1. Diagram of the study design where two 1-ba experimental treatments (bigh-impact grazing and cattle removal) were placed within a control pasture (moderate grazing). Solid lines represent fenced areas and dashed lines represent plant survey plots.

Plant Surveys

To measure plant community composition we established a permanent modified Whittaker plot (Stohlgren et al. 1995) in the center of each 1-ha treatment area for a total of nine survey plots. The modified Whittaker plot allows for determination of the heterogeneity of plant communities with a greater degree of accuracy than either true random sampling or the original Whittaker plot design (Stohlgren et al. 1995). This sampling design involved a 1000-m² plot with nested subplots consisting of 1 100-m², 2 10-m², and 10 1-m² subplots (Stohlgren et al. 1995). Species lists for the 1-, 10-, 100-, and 1000-m² subplots were completed to measure species richness; however, we only report data from 1-m² subplots here. Plant identifications were referenced with the Deaver Herbarium (Northern Arizona University in Flagstaff), and voucher specimens were retained in the Sisk Laboratory (Northern Arizona University in Flagstaff). Of the approximately 80 plant species at the site, 5 could not be identified due to the poor condition of the specimens and were removed from all analyses. In all cases unidentified specimens were rare and accounted for <0.05% of ground cover.

The first year of survey data was collected prior to implementation of the cattle removal or high-impact treatments and reflects the pretreatment condition of moderate grazing practices. Each modified Whittaker plot was surveyed annually in July, except in 1997 when measurements were made in September. Plant surveys occurred prior to the primary grazing event by cattle; however, brief periods of cattle grazing early in the season preceded plant surveys in 1997 and 1998.

Community-Level Analyses

To address our initial question of plant community responses to treatments and year effects, we created a twodimensional ordination of the plots' plant communities in species space with nonmetric multidimensional scaling (NMS; McCune & Grace 2002) for the pretreatment year of 1997 and the last year of the study, 2004. Data matrices were composed of sample units (each modified Whittaker plot) and species (number of occurrences among the ten 1-m² subplots). A Sorenson distance measure was applied because of its good performance with ecological data (McCune & Grace 2002). For each treatment the average position in ordination space of the three plots was calculated and plotted with error bars that represent standard deviation. Finally, we tested the effect size of treatment on community composition in each year with a nonmetric multiresponse permutation procedure (MRPP) and report the chance-corrected within-group agreement value (A) and a p value (McCune & Grace 2002). To further describe results from the ordination, we calculated the average cover of each plant species in

1997, the pretreatment condition, and in 2004, the last year of data collection.

To elucidate the patterns observed in the ordination, we calculated native and exotic species richness. The average species richness was calculated for each modified Whittaker plot based on the ten 1-m² subplots. We used a hierarchical approach to the statistical analysis of these data. The first step was a test of treatment-byvear interactions with a repeated measures analysis of variance (RM-ANOVA). If the result was significant (p <0.05), we conducted a post hoc analysis for treatment effects within each year with Tukey's HSD (honest significant difference, Sokal & Rohlf 1995). Nevertheless, if the treatment-by-year interaction was not significant, we report RM-ANOVA results for the whole model. A blocked design was applied to increase our ability to detect treatment effects; however, the placement of the three blocks in a single pasture (320 ha) constitutes a form of pseudo replication that we were unable to avoid due to logistics involved in moving cattle.

To investigate the potential effects of grazing intensity on the spread of exotic species of greatest concern at this site, we compared the occurrence of cheatgrass (*Bromus tectorum* L.) among treatments, as measured by frequency. We define *occurrence* as a measure of the spatial distribution of cheatgrass and calculated occurrence as the percentage of the thirty 1-m² subplots of each treatment in which cheatgrass was present. We calculated the average occurrence of cheatgrass for each treatment by year and analyzed these data as described previously.

We examined canopy cover of plant functional groups (annual forbs, perennial forbs, annual grasses, and perennial grasses) and exotic and native species. Cover was calculated in each modified Whittaker plot as the average among the 10 1-m² subplots. The 1-m² subplots were surveyed with a pin frame (Mueller-Dombois & Ellenberg 1974). We placed a pin (diameter = 0.5 cm) through the frame at 50 grid intersections for each 1-m² subplot and recorded all basal and foliar contacts with the pin. Canopy cover for each species was estimated as the number of contacts with the pin divided by 50. The pin frame method is robust to multiple observers and performs well in low-growing vegetation (Kent & Coker 1992). Statistical analysis followed methods discussed previously. Presentation of the plant functional group data followed the convention of displaying differences between alternative treatments and the moderate grazing control in each year.

Results

Grazing Effects on Plant Community Composition

In the eighth year of the study high-impact grazing had changed plant composition to a much greater extent

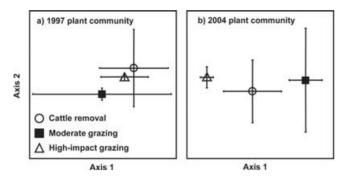


Figure 2. Ordination of plant community composition among grazing treatments in species space: (a) pretreatment condition in which all plots experience moderate grazing for at least 10 years prior (plots statistically indistinguishable; p=0.75; chance-corrected within-group agreement value, A=-0.05) and (b) plant community in the eighth year of the study (plant communities in high-impact grazing plots statistically different from either of the other treatments, p=0.02, A=0.25). Each point represents the average community composition from three treatment plots, and error bars represent the average standard deviation.

than cattle removal. Community dissimilarity between high-impact plots and moderate grazing plots was nearly twofold greater than between cattle removal and moderately grazed plots (p=0.02, A=0.25; Fig. 2b). Furthermore, high-impact grazing exerted the greatest homogenizing effect on the plant community; the average community dissimilarity was less than one-half of either cattle removal or moderate grazing plots. A more detailed description of the plant community based on canopy cover of individual species suggests that no single species is solely responsible for the community differences observed (). Pretreatment data collected in 1997 verified that plant communities were initially similar (p=0.75, A=-0.05; Fig. 2a).

Grazing Effects on Native and Exotic Plant Species Richness

Species richness of plants was affected by novel grazing treatments and interannual climatic variation. In 4 of the 7 years following initiation of the treatments, cattle removal reduced native species richness by 1 species/m² compared with the moderate grazing control (Tukey pairwise: p < 0.05; Fig. 3a). High-impact grazing yielded a similar trend, but it rarely differed statistically from the moderate grazing control. Treatment effects on native plant species richness were strongly influenced by interannual variation ($F_{14,158} = 2.40$, p < 0.01). By the final year of the study novel treatments had relatively weak effects on native species richness, which suggests that differences in native species richness were not driving the divergence

of plant communities observed in the ordination of 2004 plots (Fig. 2b).

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Differences in exotic plant species richness among treatments were an important factor in community change. Exotic species richness showed an increasing trend over time in both high-impact grazing and cattle removal treatments ($F_{14,158} = 8.48$, p < 0.01; Fig. 3b). year of the study we observed, on average, one more exotic species per square meter in cattle removal plots than the moderate grazing control and twice that amount in the high-impact grazing plots (Tukey pairwise: p < 0.05). The effect of novel treatments on exotic species was periodically overwhelmed by environmental conditions, such as during the severe early season drought of 2002, in which exotic species were nearly absent from the plots (Table 3).

Grazing Effects on Cheatgrass

Cheatgrass in particular responded strongly to the highimpact grazing treatment and to a lesser degree to the cattle removal treatment. Cheatgrass, an exotic annual grass, initially occurred in <5% of our survey plots and showed sporadic increases until it became almost completely absent during the 2002 drought ($F_{14.158} = 9.72, p < 0.01$; Fig. 4). In 2003 cheatgrass became dominant in the highimpact treatment, occurring on 80% of the 1-m² subplots, compared with <50% of plots in other treatments (Tukey pairwise: p < 0.05; Fig. 4). The difference in the spatial extent of cheatgrass between high-impact and other treatments widened in 2004: cheatgrass colonized nearly 100% of the 1-m² survey plots in the high-impact treatment. Furthermore, counts of basal and foliar cover of cheatgrass were at least two times greater in the high-impact treatment than other treatments in 2004 (M.R.R.L., data not provided).

Grazing Effects on Plant Cover

Plant cover showed greater variability in response to novel treatments than plant species richness; however, clear trends emerged. First, the effect of grazing treatments on plant cover depended on environmental conditions that fluctuate over time, such as precipitation. Treatment-by-time interactions were statistically significant for all plant functional groups (perennial forb: $F_{14,158} = 6.18, p < 0.01$; perennial grass: $F_{14,158} = 3.16$, p < 0.01; annual forb: $F_{14,148} = 3.51$, p < 0.01; annual grass: $F_{14.158} = 5.29$, p < 0.01; Fig. 5). Second, highimpact grazing generally showed greater effects on plant cover than did cattle removal. Perennial forb cover consistently declined in response to high-impact grazing in the latter half of the study and was 8% lower than in the moderate grazing control by the last year of the study (Tukey pairwise: p < 0.05; Fig. 5a). In high-impact grazing sites annual grass cover increased (Fig. 5d) but perennial

Table 2. Mean canopy cover of individual plant species prior to initiation of grazing treatments in 1997 and after 8 years of treatment in 2004.*

	Treatment						
	cattle removal		moderate grazing		high-impact grazing		
Plant species	1997	2004	1997	2004	1997	2004	
Arabis fendleri	0	0	0	0	0	<1	
Aristida purpurea	0	0	<1	<1	0	<1	
Artemisia carruthii	23	11	21	14	29	6	
Asclepias asperula	<1	0	0	<1	0	0	
Asclepias subverticillata	16	<1	15	<1	19	<1	
Astragalus sp.	<1	<1	0	0	0	<1	
Bouteloua gracilis	<1	1	4	2	1	1	
Bromus tectorum	<1	4	0	<1	<1	11	
Calochortus ambiguus	<1	0	0	0	0	0	
Cirsium wheeleri	<1	<1	<1	<1	0	<1	
Convolvulus arvensis	1	<1	0	<1	0	0	
Elymus elymoides	4	10	5	10	5	9	
Erigeron divergens	0	<1	<1	<1	0	<1	
Eriogonum racemosum	<1	1	4	<1	4	1	
Eriogonum umbellatum	0	0	<1	0	0	0	
Gutierrezia sarothrae	2	<1	1	<1	<1	<1	
Heliomeris longifolia	0	9	0	10	0	5	
Hymenoxys richardsonii	0	<1	0	<1	0	Ó	
Koeleria cristata	0	0	0	0	0	<1	
Lactuca serriola	0	<1	0	0	0	<1	
Linum aristatum	ő	0	ő	Ö	0	<1	
Lomatium nevadense	0	0	0	<1	0	0	
Lotus wrightii	0	<1	0	<1	0	0	
Lupinus kingii	0	0	0	0	0	<1	
Machaeranthera canescens	<1	<1	<1	<1	<1	<1	
Machaeranthera gracilis	0	0	0	0	0	<1	
Melilotus officinalis	3	<1	<1	<1	<1	<1	
Muhlenbergia wrightii	0	<1	0	0	0	0	
Oenothera flava	1	<1	<1	<1	<1	<1	
Orobanche fasciculata	0	<1	0	0	0	<1	
	0		0		0		
Orthocarpus purpureoalbus		<1		<1		0	
Pascopyrum smithii	11	18	11	13	9	15	
Penstemon linarioides	0	0	<1	<1	<1	<1	
Poa pratensis	0	0	0	0	0	<1	
Polygonum johnstonii	0	<1	0	<1	0	<1	
Sisymbrium altissimum	11	1	3	<1	4	1	
Sphaeralcea fendleri	<1	<1	<1	<1	0	0	
Stachys rothrockii	0	0	<1	0	<1	0	
Symphyotrichum falcatum	0	<1	0	0	0	0	
Thlaspi fendleri	0	0	0	<1	0	0	
Tragopogon dubius	0	<1	1	<1	0	2	

^{*}Values shown are the average percentage based on 30 1-m² subplots.

grass and annual forb cover did not respond consistently (Figs. 5b & 5c). Cattle removal demonstrated no consistent differences in cover from the moderate grazing control in any plant functional category (Fig. 5).

Native and exotic plant cover were also affected by alternative grazing treatments, but responses were greatly influenced by interannual variation (treatment-by-year interactions: native, $F_{14,158} = 5.70$, p < 0.01; exotic, $F_{14,158} = 5.92$, p < 0.01; Table 3). High-impact grazing had little effect on native plant cover until the sixth year of the study, when cover declined by nearly one-half in a single year, apparently due to an interaction with drought early

in the year (Tukey pairwise: p < 0.05). Two years after the sharp decline, native plant cover remained 10% lower in high-impact grazing plots than either moderate grazing or cattle removal plots.

Exotic plant cover showed the opposite response and was 13% greater in high-impact plots than the moderate grazing control in the final year of the study. Exotic cover was also greater in cattle removal plots than control plots. At the end of the study, however, it was difficult to isolate the effect of cattle removal because relatively large amounts of exotic plant cover were present in some cattle removal plots at the beginning of the study (Table 3).

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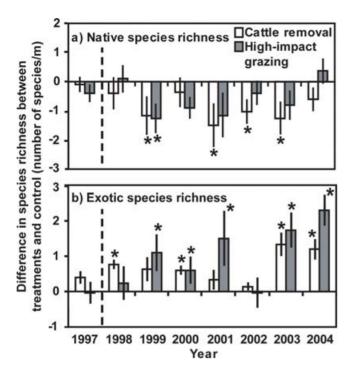


Figure 3. The (a) native and (b) exotic plant species richness among $1\text{-}m^2$ subplots under experimental grazing treatments relative to the control (reference line at 0). Experimental treatments include cattle removal and high-impact grazing, and moderate grazing represents the control. Asterisks indicate statistically significant differences (p < 0.05) and dashed lines the initiation of experimental treatments.

Discussion

The plant communities under alternative grazing treatments diverged, and the magnitude of the effect was influenced by climatic conditions. High-impact grazing in combination with a severe drought led native plant cover in the subsequent year to decline by one-half. Furthermore, we observed a sharp increase in the occurrence of annual plants, particularly cheatgrass, in the high-impact grazing treatment. By the seventh year of the study, the novel treatments of high-impact grazing and cattle removal showed greater exotic plant species richness and cover than the moderate grazing control. In general, plant cover exhibited much greater variability in response to novel grazing treatments than overall community composition, and native plant cover was relatively insensitive to the removal of cattle. In the context of an ecosystem with a century of livestock grazing, our experimental assessment of ecological effects of alternative management practices documents complex responses in the plant community that present challenges to management.

Table 3. Mean (\pm SE) canopy cover of exotic and native plant species by grazing treatment.*

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		Treatment			
Plant cover type	Year	cattle removal	moderate grazing	bigh-impact grazing	
Native	1997	60.6 (6.0)	63.8 (0.9)	69.3 (1.4)	
	1998	53.2 (7.4)	51.1 (0.7)	52.0 (2.5)	
	1999	57.2 (8.1)	58.5 (6.1)	57.8 (1.4)	
	2000	57.0 (3.2)	57.8 (1.4)	50.0 (1.4)	
	2001	59.4 (0.5)	57.0 (3.4)	54.9 (2.2)	
	2002	50.9a (3.9)	47.5a (5.8)	26.7b (0.6)	
	2003	41.9 (5.5)	41.6 (1.4)	36.9 (3.1)	
	2004	52.2a (3.2)	51.8a (1.7)	40.1b (1.8)	
Exotic	1997	15.2a (8.5)	4.5b (1.6)	4.7b (1.8)	
	1998	16.3a (8.4)	3.3b (2.9)	5.0b (1.4)	
	1999	14.1a (7.0)	3.2b (0.7)	8.8ab (1.4)	
	2000	1.2a (0.5)	0.1b(0.1)	1.0a (0.2)	
	2001	3.3ab (1.7)	1.2b (0.6)	6.1a (1.0)	
	2002	0.5 (0.2)	0.3(0.1)	0.3(0.1)	
	2003	22.2a (9.4)	11.3b (1.7)	28.2a (1.3)	
	2004	7.8b (4.4)	1.2c (0.2)	14.6a (4.2)	

^{*}Within-each-year differences among treatments differ statistically where letters are different (p < 0.05).

Climate and Grazing Interactions

The effects of alternative grazing practices were greatly influenced by interannual variation in climatic conditions, particularly precipitation. Our study spanned 8 years during which the coefficient of variation in annual precipitation was 39%, and each year's precipitation fell below the 20-year mean. Drought was particularly severe at the start

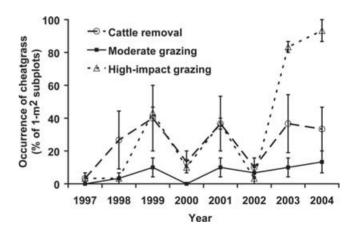


Figure 4. Average occurrence of cheatgrass (B. tectorum), an exotic grass, in 30 1- m^2 subplots, divided evenly among the three plots of each grazing treatment. A value of 100% represents maximum distribution of cheatgrass among subplots and a value of 0 represents complete absence of cheatgrass. Differences among treatments differ statistically if error bars do not overlap (p < 0.05).

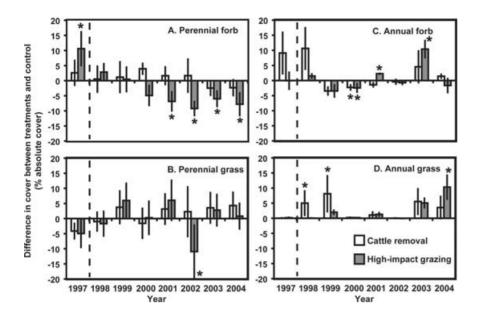


Figure 5. Foliar cover of plant functional groups compared among experimental grazing treatments and moderate grazing control: (a, b) perennial forb and grass responses to grazing treatments and (c, d) annual forb and grass responses to grazing treatments. The zero line represents the moderate grazing control, and the dashed line represents the time at which novel grazing treatments were initiated. Asterisks indicate a statistically significant difference (p < 0.05).

of the growing season in 2002, when northern Arizona received only 19% of its average precipitation (20-year mean). The drought corresponded with a 10% decline in total canopy cover for cattle removal and moderate grazing treatments and >30% decline in the high-impact treatment.

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A similar interaction of drought and heavy grazing was documented by Fuhlendorf and Smeins (1997) for the plant composition of a semiarid savanna in Texas. The plant community exposed to heavy grazing showed twofold greater change than either light grazing or cattle removal treatments (Fuhlendorf & Smeins 1997). The loss of cover measured in our study is more remarkable in light of the fact that it occurred in a year when cattle were completely absent. The drought conditions of 2002 forced ranchers to relocate their cattle, and therefore the plant response we documented provides evidence that past grazing practices can greatly influence community responses to local climatic change. In this case 5 years of high-impact grazing prior to 2002 interacted with drought to reduce plant cover dramatically.

Although canopy cover fully rebounded to predrought levels in 2003, more than one-third of this increase was attributable to exotic species. Exotic species apparently benefited from the reduced capacity of native plant species, and if the plant composition of this grassland operates in a nonequilibrium fashion (Westoby et al. 1989), the dramatic increase in exotic species may signify a transition to a new community state. In contrast, if this response is transitory, high-impact grazing practices still may present a risk to native plants because the likelihood of a future drought remains high in a region where at least eight severe, multiyear droughts have occurred in the last 1000 years (Ni et al. 2002). Predictions of future responses of the plant community to continued human perturbation, such as grazing, in the face of certain cli-

matic variability remain fraught with challenges characteristic of complex natural systems (Brown et al. 1997).

Exotic Species Responses to Grazing

Exotic cover in the last 2 years of the study was primarily composed of two annual weeds, tumblemustard (*Sisymbrium altissimum* L.) and cheatgrass, common disturbance loving species in western U.S. rangelands (Young et al. 1972; Gelbard & Belnap 2003). *S. altissimum* accounted for 13% of plant cover in 2003, which was nearly one-half of the total exotic species cover, but it declined to 1% of total plant cover in 2004. *S. altissimum* exhibited highly variable germination, which appears to be associated with wet conditions and disturbance. Cattle grazing increases *S. altissimum* abundance (Pearson 1976); however, its ability to remain a dominant species in successional communities appears limited (Daubenmire 1940).

Similarly, cheatgrass shows great interannual variability (Hull & Pechanec 1947), but a growing body of literature suggests it can alter community type and displace native biota (Young & Evans 1978; Belnap & Phillips 2001), which increases persistence of cheatgrass. Grazing is generally considered a dispersal vector for cheatgrass; however, populations can establish in locations that are not grazed by livestock (Belnap & Phillips 2001). Furthermore, carefully controlled grazing may reduce cheatgrass abundance (Daubenmire 1940; Mosley 1996). In our study region cheatgrass is broadly distributed, but seldom dominant (L. Moser, personal communication). In northern Arizona cheatgrass populations appear to be expanding in distribution along roadways (e.g., Gelbard & Belnap 2003), but it is difficult to predict the likelihood of persistence. A cheatgrass population that increased to 70% of plant cover following a wildfire in sagebrush was subsequently reduced by 65% during a period of drought (West & Yorks 2002). Our data clearly link high-impact grazing to increased spread of cheatgrass; however, the relationship between grazing and cheatgrass distribution is not necessarily linear. Our results suggest that intermediate levels of grazing may inhibit cheatgrass colonization, but this finding should be experimentally tested over a longer time period. If cheatgrass ultimately becomes a dominant species in this plant community, it would likely increase the frequency of fire, resulting in further impacts to the native biota (Young & Evans 1978).

Grazing-Tolerant Traits in the Plant Community

Surprisingly, cattle removal and high-impact grazing treatments, which were designed to represent opposing ends of a grazing intensity gradient, produced similar ecological outcomes. Both treatments reduced native species richness and increased exotic species richness in comparison with the moderate-intensity treatment. It may be that an intermediate level of disturbance from livestock grazing can promote a more heterogeneous landscape, providing greater opportunity for a variety of plants (Mc-Naughton 1983). In a review of grazing effects on vegetation heterogeneity, Adler et al. (2001) found that patchscale grazing typically increased plant diversity. Applying this framework to our study, the density of cattle in the moderate grazing treatment may have encouraged patch-scale grazing. In contrast, the high-impact treatment could be considered a homogenizing force acting on the plant community as dense cattle herds place grazers on all possible vegetative patches, equalizing ecological impacts.

Homogenization of the community may also occur at the opposite end of our gradient of grazing pressure because the removal of cattle eliminates a major agent of patch-scale disturbances. Further observation of cattle behavior at this site may provide evidence by which we may evaluate the patch-scale disturbance hypothesis. We emphasize that moderate grazing practices may sustain greater native plant diversity now, but it remains to be determined whether livestock grazing had this effect on native plant diversity during their initial introduction to this region. Undocumented changes in the populations of native grazers at the time of livestock introduction further complicate efforts to understand changes in plant communities during the past century.

An evolutionary perspective, which encompasses much longer time periods, may serve as an important indicator of plant community responses to grazing intensity (Milchunas & Lauenroth 1993). Rangelands in the American Southwest do not show evidence of large herds of native mammalian grazers equivalent to typical disturbance-adapted communities in the midwestern United States or the African Serengeti; however, its grasslands include

many disturbance-tolerant species. The dominance of short-statured plants, with perennating organs located close to the ground and storage organs located belowground, confers resilience to both drought and grazing (Coughenour 1985; Sala et al. 1996) on this grassland. Other traits, such as fiber content (Adler et al. 2004), nitrogen content (Adler et al. 2004), and ability to colonize gaps (Bullock et al. 2001), may make the system tolerant of grazing, but generalizations have been criticized (Vesk & Westoby 2001).

Within the last few centuries various events in the western United States have encouraged the spread of grazing-tolerant species. Agricultural policies have promoted "range improvement" programs that involve the seeding of grazing-tolerant species, often introducing new species (Rogler & Lorenz 1983). Moreover, extensive and intensive livestock grazing can exert directional selection pressures that favor grazing-tolerant plants over less tolerant species (Fuhlendorf et al. 2001). At our study site the grazing-tolerant bunchgrass, E. elymoides, has expanded its range within the last century and currently occurs as a dominant species across large areas (M.R.R.L., unpublished data). We hypothesize that a century of livestock grazing, and in particular a multidecadal period of intensive grazing in the late 1800s, increased the relative composition of grazing-tolerant species (Loeser et al. 2004). Incomplete records from our site also suggest that community composition has been more stable during the last half of the twentieth century, leading up to the current period of rapid spread of exotic species, which our data suggest is being facilitated by recurrent drought. In grasslands where grazing-induced shifts in dominant species have occurred, the value of a site's evolutionary history in predicting plant responses is greatly reduced.

Conclusions and Management Implications

In regions that are typified by large interannual variation in climate, interactions between grazing and climate should be anticipated by researchers and managers, even if the effects are poorly understood (Wiegand & Milton 1996; Fuhlendorf et al. 2001). In the northern Arizona rangeland, areas that have a high density of ungulates, such as corrals, watering holes, and trails, are most susceptible to exotic species expansion following severe drought, which acts as a stressor on native species. Local knowledge of management areas should be used to identify heavily grazed areas to assist managers in the control of exotic species, such as cheatgrass. Furthermore, as the variability in precipitation events is expected to increase as a component of climate change (Frich et al. 2002), managers should anticipate more drought-years that further stress native communities and facilitate the spread of cheatgrass and other exotic plant species. Although

cost-effective control of most exotic species does not appear close at hand, preventative steps are warranted. Careful scrutiny of soil disturbance events, such as intense grazing practices and road building, should precede action.

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It is a common practice in the American Southwest to remove cattle from grasslands for 1-3 years to provide an opportunity for recovery of degraded plant communities. Our results cast doubt on the efficacy of short-term removal of cattle to increase local-scale plant diversity (Floyd et al. 2003). In fact, native species richness in the moderately grazed treatment was greater or similar to that in cattle removal plots, even in very dry years. Long-term removal of cattle, perhaps on the order of decades, may yield greater responses in the native plant community. Valone et al. (2002) documented a time lag in the response of perennial grass cover to cattle removal that exceeded 20 years, and climatic conditions such as drought may further mask the effects of cattle removal (Fuhlendorf et al. 2001). Although we anticipate more profound effects of cattle removal on the plant community as this experiment matures, the recovery of native species may be inhibited by a lack of propagules. Preliminary evidence suggests that the seed bank does not include a reserve of grazingintolerant species (M.R.R.L., unpublished data), so active reseeding programs may be necessary to increase plant diversity.

We documented potential benefits to plant diversity from moderate grazing practices that may be the result of patch-scale grazing increasing community heterogeneity, but this prediction needs testing with empirical research at larger spatial scales. Indeed, animal behavior could vary with pasture size, and site-specific characteristics may modify or reverse the effect of any grazing practice. In a Californian grassland, grazing on serpentine soil increases species richness by 17%, but has the opposite effect for communities in nearby nonserpentine soils (Harrison et al. 2003). A precautionary approach to conserving biodiversity may warrant the application of multiple strategies to achieve greater landscape heterogeneity (Christensen 1997; Wiens 1997). Fuhlendorf and Engle (2001) recommend a landscape-scale approach that applies a heterogeneous patchwork of disturbance, such as grazing or fire, followed by periods of rest. Results of the application of this approach in the mesic tallgrass prairie show landscape-scale increases in plant diversity (Fuhlendorf & Engle 2001), but data are limited for dry-land regions. Our results suggest that the combined species richness in cattle removal and moderate grazing treatments could exceed the species richness of moderate grazing alone; however the response was inconsistent. The site-specific qualities of plant composition, soil type, and climatic conditions present a challenge to conservation planning that may be best addressed with on-site experimentation with management actions, such as demonstrated here for a semiarid southwestern grassland.

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Literature Cited

- Adler, P. B., D. A. Raff, and W. K. Lauenroth. 2001. The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465-479.
- Adler, P. B., D. G. Milchunas, W. K. Lauenroth, O. E. Sala, and I. C. Burke. 2004. Functional traits of graminoids in semi-arid steppes: a test of grazing histories. Journal of Applied Ecology 41:653–663.
- Belnap, J., and S. L. Phillips. 2001. Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. Ecological Applications 11:1261–1275.
- Bock, C. E., J. H. Bock, and H. M. Smith. 1993. Proposal for a system of federal livestock exclosures on public rangelands in the western United States. Conservation Biology 7:731-733.
- Brown, D. E. 1994. Biotic communities: southwestern United States and northwestern Mexico. University of Utah Press, Salt Lake City.
- Brown, J. H., and W. McDonald. 1995. Livestock grazing and conservation on southwestern rangelands. Conservation Biology 9:1644-1647
- Brown, J. H., T. J. Valone, and C. G. Curtin. 1997. Reorganization of an arid ecosystem in response to recent climate change. Proceedings of the National Academy of Sciences of the United States of America 94:9729–9733.
- Bullock, J. M., J. Franklin, M. J. Stevenson, J. Silvertown, S. J. Coulson, S. J. Gregory, and R. Tofts. 2001. A plant trait analysis of responses to grazing in a long-term experiment. Journal of Applied Ecology 38:253–267.
- Christensen, N. L. 1997. Managing for heterogeneity and complexity on dynamic landscapes. Pages 167-186 in S. T. A. Pickett, R. S. Ostfeld, M. Shachak, and G. E. Likens, editors. The ecological basis for conservation: heterogeneity, ecosystems, and biodiversity. Chapman and Hall, New York.
- Coughenour, M. B. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. Annals of the Missouri Botanical Garden 72:852–863.
- Curtin, C. G. 2002. Livestock grazing, rest, and restoration in arid landscapes. Conservation Biology 16:840-842.
- Curtin, C. G., N. F. Sayre, and B. D. Lane. 2002. Transformations of the Chihuahuan Borderlands: grazing, fragmentation, and biodiversity conservation in desert grasslands. Environmental Science and Policy 5:55–68
- Daubenmire, R. F. 1940. Plant succession due to overgrazing in the Agropyron bunchgrass prairie of southeastern Washington. Ecology 21:55-64.

Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. Conservation Biology 8:629-644.

- Floyd, M. L., T. L. Fleischner, D. Hanna, and P. Whitefield. 2003. Effects of historic livestock grazing on vegetation at Chaco Culture National Historic Park, New Mexico. Conservation Biology 17:1-9.
- Frich, P., L. V. Alexander, P. Della-Marta, B. Gleason, M. Haylock, A. M. G. Klein Tank, and T. Peterson. 2002. Observed coherent changes in climatic extremes during the second half of the twentieth century. Climate Research 19:193–212.
- Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. BioScience 51:625–632.
- Fuhlendorf, S. D., and F. E. Smeins. 1997. Long-term vegetation dynamics mediated by herbivores, weather, and fire in a *Juniperus-Quercus* savanna. Journal of Vegetation Science 8:819–828.
- Fuhlendorf, S. D., D. D. Briske, and F. E. Smeins. 2001. Herbaceous vegetation change in variable rangeland environments: the relative contribution of grazing and climatic variability. Applied Vegetation Science 4:177-188.
- Gelbard, J. L., and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology 17:420– 432.
- Harrison, S., B. D. Inouye, and H. D. Safford. 2003. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. Conservation Biology 17:837–845.
- Hastings, J. R., and R. M. Turner. 1965. The changing mile: an ecological study of vegetation change with time in the lower mile of an arid and semiarid region. University of Arizona Press, Tucson.
- Hull, A. C., and J. F. Pechanec. 1947. Cheatgrass—a challenge to range research. Journal of Forestry 45:555–564.
- Jones, A. 2000. Effects of cattle grazing on North American arid ecosystems: a quantitative review. Western North American Naturalist 60:155-164.
- Kent, M., and P. Coker. 1992. Vegetation description and analysis: a practical approach. CRC Press, Boca Raton, Florida.
- Loeser, M. R., T. D. Sisk, and T. E. Crews. 2001a. Plant community responses to livestock grazing: an assessment of alternative management practices in a semi-arid grassland. Pages 188 in R. K. Vance, C. B. Edminster, W. W. Covington, and J. A. Blake, editors. Ponderosa pine ecosystems restoration and conservation: steps toward stewardship. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Flagstaff, Arizona.
- Loeser, M. R., T. D. Sisk, T. E. Crews, K. Olsen, C. Moran, and C. Hudenko. 2001b. Reframing the grazing debate: evaluating ecological sustainability and bioregional food production. Pages 3–18 in C. W. van Riper III, K. A. Thomas, and M. A. Stuart, editors. Proceedings of the fifth biennial conference of research on the edorado plateau. U.S. Geological Survey, Colorado Plateau Field Station, Flagstaff, Arizona.
- Loeser, M. R., T. E. Crews, and T. D. Sisk. 2004. Defoliation increased above-ground productivity in a semi-arid grassland. Journal of Range Management 57:442-447.
- Loeser, M. R., S. D. Mezulis, T. D. Sisk, and T. C. Theimer. 2005. Vegetation cover and forb responses to cattle exclusion: implications for pronghorn. Rangeland Ecology and Management 58:234–238.
- Mack, R. N., and J. N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. The American Naturalist 119:757-773.

Maestas, J. D., R. L. Knight, and W. C. Gilgert. 2003. Biodiversity across a rural land-use gradient. Conservation Biology 17:1425–1434.

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- McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MiM Software Design, Gleneden Beach, Oregon.
- McNaughton, S. J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. Ecological Monographs 53:291–320.
- Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:327–366.
- Mosley, J. C. 1996. Prescribed sheep grazing to suppress cheatgrass: a review. Sheep and Goat Research Journal 12:74-81.
- Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods in vegetation ecology. John Wiley and Sons, New York.
- Ni, F., T. Cavazos, M. K. Hughes, A. C. Comrie, and G. Funkhouser. 2002. Cool-season precipitation in the southwestern USA since AD 1000: comparison of linear and nonlinear techniques for reconstruction. International Journal of Climatology 22:1645–1662.
- Pearson, L. C. 1976. Primary production in grazed and ungrazed desert communities of eastern Idaho. Ecology 46:278–285.
- Rogler, G. A., and R. J. Lorenz. 1983. Crested wheatgrass—early history in the United States. Journal of Range Management 36:91-93.
- Sala, O. E., W. K. Lauenroth, S. J. McNaughton, G. Rusch, and X. Zhang. 1996. Biodiversity and ecosystem functioning in grasslands. Pages 129-149 in H. A. Mooney, J. H. Cushman, E. Medina, O. E. Sala, and E.-D. Schulze, editors. Functional roles of biodiversity: a global perspective. John Wiley and Sons, New York.
- Savory, A., and S. D. Parsons. 1980. The Savory grazing method. Rangelands 2:234-237.
- Sokal, R. R., and F. J. Rohlf. 1995. Biometry. W.H. Freeman, New York.
 Stohlgren, T. J., M. B. Falkner, and L. D. Schell. 1995. A modified-Whittaker nested vegetation sampling method. Vegetatio 117:113-121
- Stohlgren, T. J., L. D. Schell, and B. Vanden Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in rocky mountain grasslands. Ecological Applications 9:45-64.
- Valone, T. J., M. Meyer, J. H. Brown, and R. M. Chew. 2002. Timescale of perennial grass recovery in desertified arid grasslands following livestock removal. Conservation Biology 16:995–1002.
- Vesk, P. A., and M. Westoby. 2001. Predicting plant species' responses to grazing. Journal of Applied Ecology 38:897–909.
- West, N. E., and T. P. Yorks. 2002. Vegetation responses following wildlife on grazed and ungrazed sagebrush semi-desert. Journal of Range Management 55:171-181.
- Westoby, M., B. Walker, and I. Noy-Meir. 1989. Range management on the basis of a model which does not seek to establish equilibrium. Journal of Arid Environments 17:235–239.
- Wiegand, T., and S. J. Milton. 1996. Vegetation change in semiarid communities. Vegetatio 125:169-183.
- Wiens, J. A. 1997. The emerging role of patchiness in conservation biology. Pages 93–107 in S. T. A. Pickett, R. S. Ostfeld, M. Shachak, and G. E. Likens, editors. The ecological basis for conservation: heterogeneity, ecosystems, and biodiversity. Chapman and Hall, New York.
- Young, J. A., and R. A. Evans. 1978. Population dynamics after wildfires in sagebrush grasslands. Journal of Range Management 31:283–289.
- Young, J. A., R. A. Evans, and J. Major. 1972. Alien plants in the Great Basin. Journal of Range Management 25:194-201.